

***Hydrolagus mccoskeri* sp. nov., a new species of chimaeroid fish from the Galápagos Islands (Holocephali: Chimaeriformes: Chimaeridae)**

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Abstract

A new species of chimaeroid, *Hydrolagus mccoskeri* sp. nov., is described from the Galápagos Islands. This species represents the second member of the family Chimaeridae known from the eastern equatorial Pacific. It can be distinguished from its congeners by a combination of the following characters: small head with short, blunt snout; preopercular and oral lateral line canals branching from the same node off the infraorbital canal and sharing a short common branch; dorsum medium brown with numerous narrow, sharply delineated circular and elongate white blotches; ventrum white to tan with extremely fine brown mottling. The species is compared to *Hydrolagus novaezealandiae* and *Hydrolagus collieri*, the most similar congeners in color pattern and morphology.

Key words: Chimaeriformes, Chimaeridae, *Hydrolagus*, Galápagos

Introduction

Chimaeroids are the extant members of the subclass Holocephali (living and fossil chimaeras or ratfishes) which, together with the Elasmobranchii (sharks, skates and rays), form the monophyletic class Chondrichthyes (Didier 1995; Grogan & Lund 2004; Maisey 1984, 1986; Schaeffer 1981). Their distribution is cosmopolitan with the exception of the Arctic and Antarctic oceans. At present there are 34 species described in the order Chimaeriformes (Compagno 2005), with as many as ten new species awaiting formal

description, all within the family Chimaeridae (Didier, unpublished data). One additional species, *Hydrolagus lusitanicus* Moura *et al.* 2005, was recently described but it remains unclear whether or not this is indeed a valid species (D.A. Didier, personal observation). The Chimaeridae are the largest family of the order, consisting of two genera, *Chimaera* and *Hydrolagus*. The *Hydrolagus* are more speciose and differentiated from *Chimaera* by the absence of a notch separating the anal fin from the ventral caudal fin.

Species richness of *Hydrolagus* is greatest in the western Pacific, with 11 known species. The eastern Pacific fauna consists of only two described species, *Hydrolagus colliei* (Lay & Bennett 1839) and *H. macrophthalmus* de Buen 1959. The former is endemic to the eastern North Pacific (Allen & Smith 1988; Didier & Rosenberger 2002; Eschmeyer *et al.* 1983; Miller & Lea 1972), while the latter seems to be restricted to the eastern South Pacific. The only confirmed records of *H. macrophthalmus* are from off Chile (de Buen 1959), however, reports of this species from off Peru (Chirichigno 1968) may also be accurate (Quaranta *et al.* in review). The new species described in this study marks the first record of a chimaeroid from the Galápagos Islands (Grove & Lavenberg 1997).

The discovery of chimaeras within the Galápagos archipelago is likely due to improvements in sampling technology. The steep slopes and rough volcanic terrain characteristic of deep-water environments in the archipelago have impeded thorough investigation of fish communities using traditional trawling methods. However, the use of manned submersibles along the volcanic slopes of the Galápagos Islands has facilitated the discovery of new species and range extensions (McCosker 1997; McCosker *et al.* 1997), including the new species of *Hydrolagus* described herein.

Methods and materials

Type specimens (n = 2) were collected by the submersible *Johnson Sea-Link II* (JSL) and its attending vessel, the *R/V Seward Johnson* (operated by the Harbor Branch Oceanographic Institution, HBOI), in a joint expedition led by John E. McCosker of the California Academy of Sciences (CAS) during November 1995 and June–July 1998. The submersible hovered near the bottom and scanned the seafloor for marine life using xenon arc lights which had the ability to illuminate specimens in near-daylight true color for photography, and to ready them for capture. Observations of specimens prior to capture allowed for their behavior and live coloration to be recorded *in situ*. Specimens were collected by a maneuverable suction hose, allowing individuals to survive and retain fresh coloration and natural morphology for observation at the surface.

Preserved specimens were used for morphological measurements. Point-to-point measurements were performed with a dial caliper and measuring tape. Definitions of measurements and their acronyms are based on the methodology described by Didier & Stehmann (1996), as modified from Compagno *et al.* (1990). Measurements follow Didier

& Séret (2002), a scheme explicit to the genus *Hydrolagus*. Terminology of tooth plates follows Didier *et al.* (1994) and Patterson (1992). Body measurements are as follows: total length (TL); precaudal length (PCL), distal tip of snout to the origin of the dorsal lobe of the caudal fin; body length (BDL), dorsal edge of gill opening to origin of dorsal lobe of the caudal fin; snout-vent length (SVL), distal tip of snout to the external opening of the gastrointestinal tract; trunk length (TRL), ventral edge of gill opening to the external opening of the gastrointestinal tract; pre-second dorsal length (PD2); pre-first dorsal length (PD1); pre-oral length (POR), snout tip to end of upper labial fold; pre-narial length (PRN), snout tip to anterior edge of nasal apertures; pre-orbital length (POB), distal tip of snout to anterior edge of orbit; second dorsal-fin base (D2B); maximum height of anterior lobe of second dorsal fin (D2AH); maximum height of posterior lobe of second dorsal fin (D2PH); first dorsal-fin base (D1B), from anterior edge of fin spine to insertion of first dorsal fin (D1B); maximum height of first dorsal fin (D1H), from the insertion to distal tip of first dorsal; dorsal caudal margin length (CDM) from origin to insertion of dorsal caudal lobe; maximum height of dorsal lobe of caudal fin (CDH); ventral caudal margin (CVM) from origin to insertion of ventral caudal lobe; total caudal length (CTL), from origin of dorsal caudal lobe to end of caudal filament; maximum height of ventral lobe of caudal fin (CVH); head length (HDL), from distal tip of snout to dorsal edge of gill opening; anterior margin of pectoral-fin (P1A); anterior margin of pelvic fin (P2A); interdorsal space (IDS); dorsal-caudal space (DCS); anterior edge of first dorsal fin base to anterior edge of pectoral fin lobe (point at which fin lobe attaches to pectoral girdle; D1P1); origin of second dorsal fin to anterior edge of pectoral fin lobe (D2P1); origin of second dorsal fin to anterior edge of pelvic fin lobe (D2P2); eye length (EYL); eye height (EYH).

Measurements of the lateral line canals of the head follow the methodology and terminology of Didier & Séret (2002) and are described as follows: distance from anterior oronasal fold to center of nasal canal (ONC); length of the rostral canal (LRC); length of the nasal canal measured as a straight-line distance from the right to left side (LNC); distance between infraorbital and angular canal measured as the straight-line distance from the junction of the oral and infraorbital to the junction of the oral and angular canal (IOA); distance between preopercular canal and main trunk canal measured from their junction with the infraorbital canal (OTM); distance between the main trunk canal and supratemporal canal measured from their junctions with the infraorbital and postorbital canals, respectively (OCL); length of the supratemporal canal measured across the head from its junctions with the postorbital canal (STL); distance from anterior base of spine to the center of the supratemporal canal (SPS).

Institutional abbreviations follow Leviton *et al.* (1985).

***Hydrolagus mccoskeri* sp. nov.**

Galápagos Ghost Shark

(Figs. 1–3)

Holotype. CAS 86558, juvenile female, 381 mm TL, 274 mm PCL, 211 mm BDL, Southeast of San Cristóbal Island, Galápagos, (01°5.981'S, 89°12.235'W), 396.24 m, coll. by John E. McCosker (CAS), R. Grant Gilmore (HBOI) & Bruce Robison (MBARI), 17 Nov. 1995 (JSL dive 3934).

Paratype. CAS 223971, juvenile female, 227 mm TL, 138 mm PCL, 107 mm BDL, off Isla Española, Galápagos, (01°18.5'S, 89°45.5'W), 505.97 m, coll. by John E. McCosker (CAS), and John Ross (Smithsonian Magazine), 6 Jul. 1998 (JSL dive 3094).

Diagnosis. A species of *Hydrolagus* distinguished from congeners by the following combination of characters: head small with short, blunt snout; second dorsal fin only slightly indented along its length; preopercular and oral lateral line canals branching from the same node off the infraorbital canal and sharing a short common branch; dorsum medium brown with numerous narrow, sharply delineated irregular circular and elongate white blotches; ventrum white to tan with extremely fine brown mottling.

Description. Holotype and paratype morphometric measurements are presented in Table 1. Head small (HDL 31–32 % BDL), with rounded, short snout and large eyes (EYL 9–13 % BDL). Body depth (dorso-ventral height of body at a given distance from snout tip) remains similar from head to origin of pelvic fins, from which point it rapidly tapers distally to pelvic fin tips (when depressed posteriorly), subsequently transitioning into a whiplike tail. Skin firm and robust, not deciduous as in some other *Hydrolagus* (Didier 2002). Post-anal pad present, but inconspicuous in the juvenile type specimens.

Tooth plates light yellow in preserved specimens, with white tritors. Vomerine tooth plates small and incisor-like with 5 tritors visible on the right and 5–6 on the left. Palatine tooth plates with 2–3 tritors along the oral surface originating at the posterior edge and terminating prior to the anterior edge. Small protrusions are present along the anterior labial edge. Mandibular tooth plates incisor-like and large (three times wider than vomerine tooth plates), with 5 tritors per side.

Lateral line canals on head are open grooves with especially wide dilation of canals on the snout. Preopercular and oral lateral line canals branch from the same node off the infraorbital canal and share a short common branch (Fig. 4). Lateral line of the trunk and tail is fairly straight, with very small asymmetrical undulations and a sigmoid curve at the point where it meets the canals of the head.

First dorsal fin preceded by a highly robust dorsal spine, which is triangular in cross section. Two narrowly spaced columns of serrations are present on the posterolateral edges of the distal 2/3–3/4 of spine. Spine only slightly curved posteriorly, with the majority of curvature occurring in the distal 1/3 of spine. First dorsal fin nearly triangular, with a straight posterior margin and slightly convex anterior margin. Second dorsal fin slightly indented along its length with the anterior lobe higher than posterior lobe. Dorsal and

ventral caudal fin lobes elongate, with a longer ventral caudal fin lobe extending anteriorly. Anterior portion of the ventral caudal fin lobe merges into a fleshy ridge. The ridge extends anteriorly an additional 26% of body length and is nearly aligned vertically with the midpoint of the second dorsal fin. Both caudal fin lobes are approximately equal in height. Caudal filament moderately stout. No anal fin present.

Anterior margin of pectoral fin slightly convex, with increasing curvature toward an acutely pointed distal tip. Posterior margin straight, becoming concave at distal 1/4 of length. Pectoral fins, when depressed posteriorly, reach past the pelvic fin insertion and distal tip of pelvic fin lobe. Pelvic fins large and nearly triangular. Anterior margin slightly convex, particularly at distal 1/3. Posterior margin nearly straight, but very slightly convex. Distal tip slightly rounded to acutely pointed.

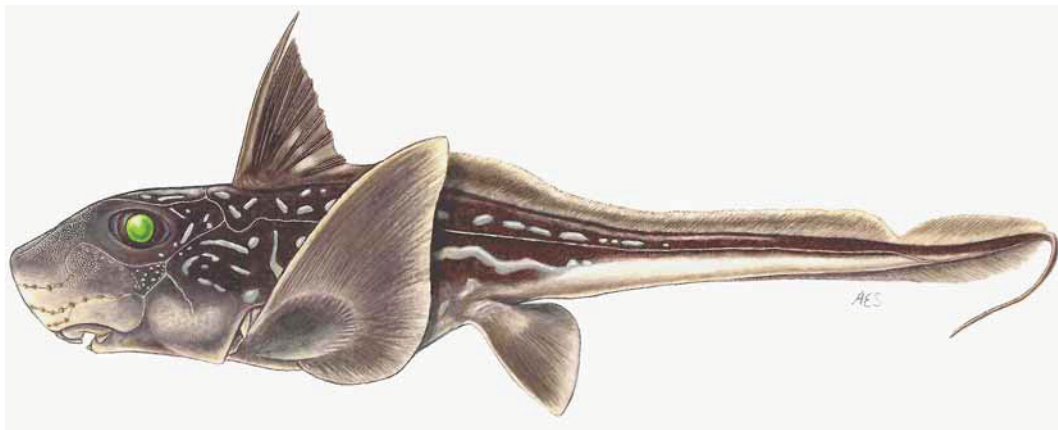


FIGURE 1. Drawing of *Hydrolagus mccoskeri* sp. nov., holotype, CAS 86558, juvenile, 381 mm TL, 211 mm BDL, courtesy of Alison Schroeer, based on preserved specimen and description of live coloration.



FIGURE 2. Photograph of preserved *Hydrolagus mccoskeri* sp. nov., holotype, CAS 86558, juvenile, 381 mm TL, 211 mm BDL.

Coloration. Life color of the holotype is an overall medium gray on dorsal and lateral sides extending to near the ventrum, with slight superficial silvery sheen; snout and oral

region slightly lighter gray; ventrum light gray to whitish, with underside of caudal region from the pelvic insertion to the terminal end of the tail whitish, except for the dark gray caudal filament; first dorsal fin dark gray with slightly lighter gray areas in membranes between proximal ceratotrichia; second dorsal fin with white proximal and distal margin bordering a medial dark gray stripe; pectoral and pelvic fins darkish gray on lateral portion, slightly lighter gray on medial portion, with whitish posterior margin; dorsum between the eyes and the anterior caudal region is profusely marked with irregular but well-defined spots, vermiculations, and stripes of a silvery white; pigment around the outer margins of the eye is dark grey and the tapetum lucidum reflects an emerald-green.

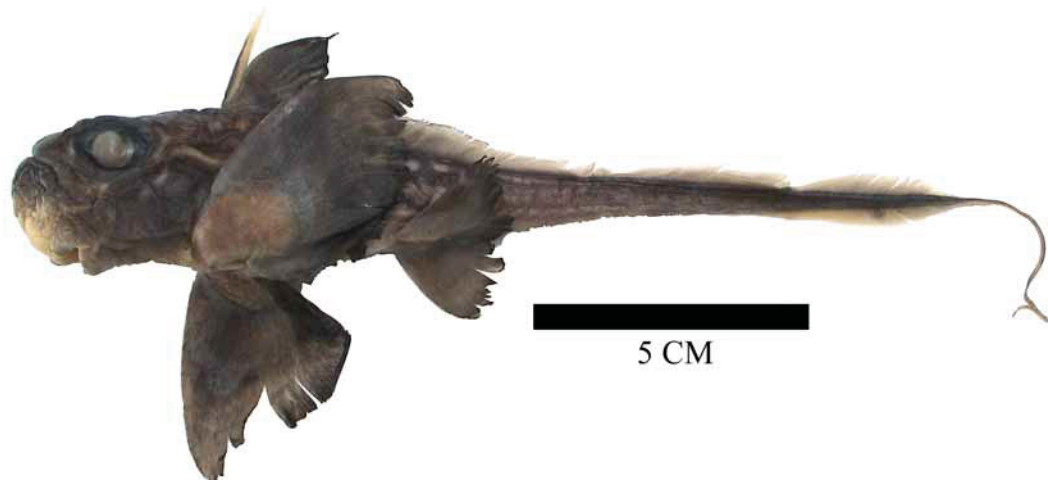


FIGURE 3. Photograph of preserved *Hydrolagus mccoskeri* sp. nov., paratype, CAS 223971, juvenile, 227 mm TL, 107 mm BDL.

Color of preserved holotype is medium brown on the dorsum with numerous irregular, finely delineated rounded to elongate white blotches. Rostrum is a uniform medium brown dorsally and uniform tan from snout tip to mouth. Coloration of the head and trunk ventral to the dorsal edge of gill opening is a uniform white to tan with fine brown mottling, with finer mottling at the head, creating a uniform light brown appearance. On the tail, this lighter ventral coloration begins below the lateral line.

Medial portion of paired fin lobes uniform medium brown, fading to off-white with fine brown mottling at the fin bases and lateral portion of fin lobes. Paired fin webs light brown to grey-brown, darkest at anterior margin, fading to a translucent posterior margin. Second dorsal fin and dorsal caudal fin lobe are uniform medium brown, bordered by a light colored proximal margin and a translucent distal margin. Ventral caudal fin lobe is uniform medium brown, fading to tan anteriorly. Coloration of preserved paratype is similar to holotype, with a few exceptions: coloration of paired fin webs is uniform, without a darkened anterior margin; hue of the body is darker, particularly on the ventrum; color pattern of second dorsal fin and dorsal caudal fin lobe is much less distinct and the

hue is light brown instead of medium brown.

Etymology. The Latin name is designated in honor of Dr. John E. McCosker, a renowned ichthyologist who collected and graciously provided the type specimens. The common name is an allusion to the known distribution of the species.

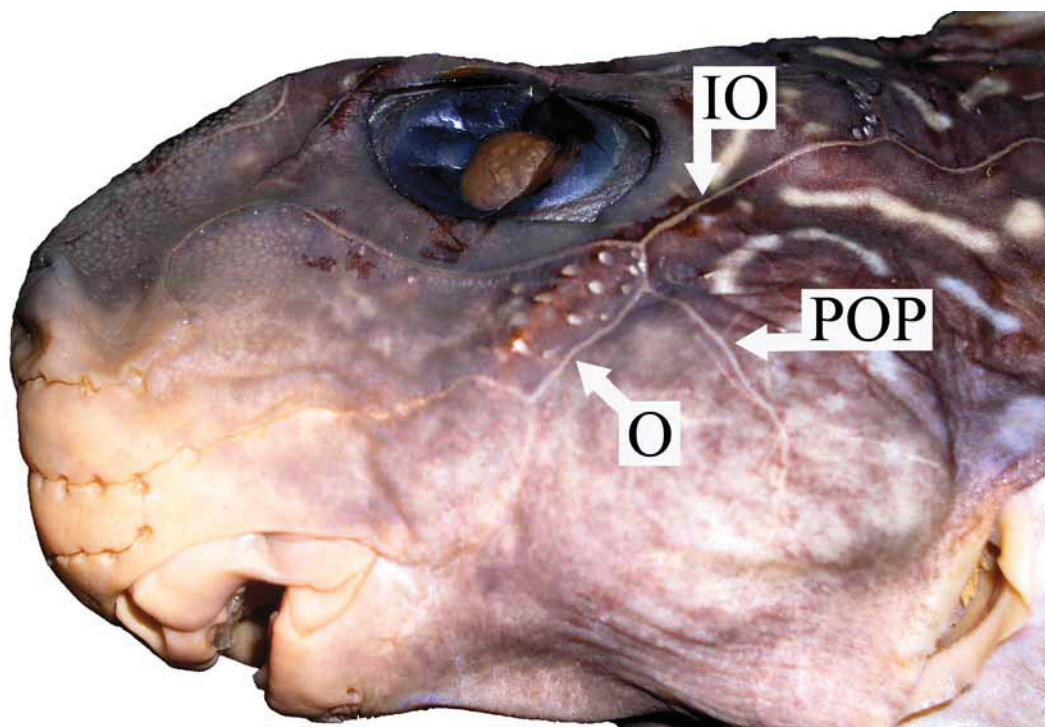


FIGURE 4. Photograph of lateral line canals on the head of preserved *Hydrolagus mccoskeri* sp. nov. holotype. The preopercular (POP) and oral (O) lateral line canals branch from the same node off the infraorbital (IO) canal and share a short common branch.

Distribution and Ecology. Nine specimens were observed from four sites in the Galápagos archipelago: Cabo Douglas, Fernandina Island (01°17.534'S, 91°38.852'W), Isla Española (01°18.5335'S, 89°45.4037'W), Marchena Island (00°24.0'N, 90°26.5'W) and San Cristóbal Island (01°5.981'S, 89°12.235'W), at 396.24–505.97 m depth. Individuals were found alone or in groups along steep slopes, within a few meters of the seafloor. Habitat was composed of igneous boulders, cobbles, and pebbles.

The observed bathymetric range is shallow compared to many other *Hydrolagus*, and may reflect incomplete deep-water sampling in the region. However, the two most similar congeners in morphology and distribution, *H. novaezealandiae* and *H. colliei*, are also found in relatively shallow depths (Eschmeyer *et al.* 1983; Anderson *et al.* 1998), suggesting that the observed depth distribution of *H. mccoskeri* may accurately represent its true bathymetric range.

TABLE 1. Range of measurements and proportions of body length (%BDL) for comparative and type material (data for *H. collieri* from Didier & Rosenberger 2002).

	<i>H. mccoskeri</i> sp. nov.				Comparative material			
	Holotype		Paratype		<i>H. novaezealandiae</i>		<i>H. collieri</i>	
	CAS 86558		CAS 223971		n = 11 (4 females, 7 males)		n = 59 (38 females, 21 males)	
	mm	%BDL	mm	%BDL	mm	%BDL	mm	%BDL
TL	381	181	227	212	480–762	154–236	123–583	139–225
PCL	274	130	138	129	375–552	123–132	78.3–457	123–147
BDL	211	—	107	—	288–432	—	59.5–359	—
SVL	142	67	69	64	187–282	58–68	40–275	67–93
D1P1	45.6	22	23.0	21	59–90	19–23	12.1–105	20–34
D1P2	81.7	39	38.2	36	115–185	38–46	23.3–165	39–52
D2P1	57.6	27	31.4	29	94–160	31–40	23.4–162	37–53
TRL	83.2	39	41	38	105–172	34–43	22.9–180	38–55
PD2	113	54	58	54	177–256	58–67	46–253	40–88
PD1	64	30	37	35	100–142	31–40	23.1–138	21–53
POB	25	12	12.0	11	40–57	11–16	6.7–65	11–23
D2B	163	77	78.2	73	122–286	40–69	37.2–217	57–72
D2AH	12.7	6	5.8	5	11.8–20.0	4–5	7.0–23	5–10
D2PH	8.8	4	3.5	3	10.4–16.0	3–4	2.0–16	1–7
D2MH	6.9	3	2.6	2	—	—	—	—
D1B	37.2	18	18.4	17	51.3–69.8	16–19	11.8–72.4	15–26
DSA	60.5	29	22.5	21	61.3–89.8	20–23	15.8–100	22–31
D1H	46.6	22	23.7	22	58.7–83.3	17–22	12.3–89.4	17–30
CDM	63.8	30	32.4	30	64–80	16–26	4–142	24–68
CDH	8.4	4	4.2	4	7.7–12.7	2–3	3–15	2–6
CVM	75.2	36	28.4	27	70–87	17–28	25.3–152	26–91
CVH	8.1	4	3.3	3	7.0–12.2	2–3	3–14	2–5
CPH	7.2	3	4.2	4	7.0–10.8	2–3	—	—
HDL	67	32	33.4	31	83–135	26–32	17.8–125	26–45
P1A	85.9	41	48.7	45	105–162	35–39	22.2–130	31–46
P2A	52.3	25	25.0	23	68–90	20–24	18–80	18–31
IDS	16.0	8	6.6	6	32.5–62.7	11–15	5.5–71.6	9–21
DCS	2.4	1	2.5	2	—	—	1.0–6.8	1–3
EYL	19.8	9	13.8	13	21.8–33.6	7–10	7.2–30	7–16
EYH	13.7	6	8.5	8	15.1–23.9	5–6	5.0–21	5–10

to be continued.

TABLE 1 (continued).

	<i>H. mccoskeri</i> sp. nov.				Comparative material			
	Holotype		Paratype		<i>H. novaezealandiae</i>		<i>H. colliei</i>	
	CAS 86558		CAS 223971		n = 11 (4 females, 7 males)		n = 59 (38 females, 21 males)	
	mm	%BDL	mm	%BDL	mm	%BDL	mm	%BDL
CTL	104.1	49	80.5	75	112–310	27–105	—	—
POR	25.4	12	18.7	17	37–58	12–18	—	—
PRN	15.6	7	13.5	13	17–35	5–10	—	—
D2P2	51.1	24	20.2	19	50–90	16–23	9.9–80	17–27
ONC	5.3	3	3.8	4	6.0–11.5	2–3	—	—
LRC	2.6	1	1.8	2	—	—	—	—
LNC	17.6	8	10.6	10	18.0–29.3	6–7	—	—
IOA	13.5	6	6.5	6	11.0–17.9	3–6	—	—
OTM	23.0	11	12.8	12	25.7–42.0	8–10	—	—
OCL	11.5	5	6.5	6	12.7–17.9	4–5	—	—
STL	12.6	6	6.5	6	12.0–17.0	3–5	—	—
SPS	8.0	4	4.7	4	12.9–27.1	4–6	—	—

We suggest *H. mccoskeri* is likely endemic to the Galápagos archipelago. There is a high degree of endemism in this geographic region due to its isolation from the South American continent (Grove & Lavenberg 1997; McCosker 1998). The Galápagos archipelago has never been closer to the South American continent than today (Cox 1983). The expanse of deep water extending thousands of kilometers to the east and west, the East Pacific Barrier (Ekman 1953), has effectively contained many species within this small area. Given this species' apparently shallow bathymetric range and limited vagility, we hypothesize that this new species of *Hydrolagus* represents another of these species limited in its distribution.

Comparison. *Hydrolagus mccoskeri* is the third species of *Hydrolagus* described from the eastern Pacific. It is easily distinguished from its nearest geographic relatives, *H. macrophthalmus* and *H. colliei*. *Hydrolagus macrophthalmus* is an even brown color with no distinct color pattern (de Buen 1959; Quaranta *et al.* in prep.). *Hydrolagus colliei* is characterized by a reddish-brown color with distinct white spots, a second dorsal fin that is deeply indented, almost separated into two parts, and oral and preopercular lateral line canals that originate separately from the infraorbital canal (Didier & Rosenberger 2002). The body of *H. colliei* anterior to the external opening of the gastrointestinal tract is longer than in *H. mccoskeri* (Table 1; SVL 67–93% BDL, and TRL 38–55% BDL).

An additional variant of *Hydrolagus*, collected from the Galápagos archipelago during this survey, is easily distinguished from *H. mccoskeri* by a longer trunk length (TRL), deeper

body (D1P1, D2P1), shorter second dorsal fin (D2B) and caudal dorsal margin (CDM), shorter head length (HDL), and greater height of the anterior lobe of the second dorsal fin (D2AH) (Quaranta *et al.* in review). Coloration is dark brown to black, with a white blotch on the midpoint of the second dorsal fin, occasionally with a few large oval white blotches on the lateral sides of the body, but not as extensive as in *H. mccoskeri*. This morphotype is likely a new species, however, its similarity to *H. macrophthalmus* is being addressed in a subsequent study (Quaranta *et al.* in review).

Hydrolagus mccoskeri most closely resembles *H. novaezealandiae*, a species endemic to the coast of New Zealand. However, the white markings on the dorsum of *H. mccoskeri* are more numerous, less continuous and more sharply delineated. The oral and preopercular lateral line canals of *H. mccoskeri* branch from the same node off the infraorbital canal and share a short common branch, whereas in *H. novaezealandiae* and *H. colliei*, they branch from separate nodes off the infraorbital canal. There are also distinct morphological differences that differentiate these species (Table 1). In particular, *H. mccoskeri* has a shorter, blunter head and snout (POB 11-12% BDL), and the origin of the second dorsal fin is further anterior. Additionally, the majority (86%) of lateral line canals along the head are greater in length in *H. mccoskeri*.

Remarks. Determination of chimaeroid taxonomy is difficult because of extensive interspecific similarity in morphology and poor condition of type specimens captured by traditional fishing gear. This study demonstrates the benefits of using submersibles as a method of taxonomic research, allowing identification of a new species from limited type material while yielding accurate and precise information on live body color, behavior, distribution, and habitat associations that would be otherwise unavailable from deep waters. The condition of the type specimens facilitated the analysis of characters considered to be conservative and robust for the distinction of chimaeroid species. These characters include color pattern, shape of the fins and body (Didier 1998), and lateral line morphology (Didier & Nakaya 1999). The type of branching of the oral and preopercular lateral line canals from the infraorbital canal has been found to be particularly useful in the taxonomy of chimaeras (Didier & Nakaya 1999; Didier & Séret 2002).

Comparative material. *Hydrolagus novaezealandiae*, 11 specimens—ANSP 174646-4, male, 715 mm TL, 505 mm PCL, 410 mm BDL; ANSP 174646-5, female, 655 mm TL, 388 mm PCL, 300 mm BDL; ANSP 174646-6, male, 670 mm TL, 440 mm PCL, 348 mm BDL; ANSP 174646-7, female, 700 mm TL, 552 mm PCL, 432 mm BDL; ANSP 174646-8, male, 655 mm TL, 533 mm PCL, 425 mm BDL; ANSP 174646-9, female, 698 mm TL, 390 mm PCL, 296 mm BDL; ANSP 174646-10, male, 480 mm TL, 375 mm PCL, 288 mm BDL; ANSP 174646-11, female, 650 mm TL, 384 mm PCL, 303 mm BDL; ANSP 174646-12, male, 614 mm TL, 454 mm PCL, 365 mm BDL; ANSP 174646-14, male, 762 mm TL, 487 mm PCL, 373 mm BDL; ANSP 174646-15, male, 635 mm TL, 393 mm PCL, 306 mm BDL; all from Northern Campbell Plateau, New Zealand (48°55.02–55.08'S, 167°2.75–7.29'E), 03 Mar. 1995, GRV “TANGAROA” (cruise TAN 9502/095).

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References

- Allen, M.J. & Smith, G.B. (1988) *Atlas and Zoogeography of Common Fishes in the Bering Sea and Northeastern Pacific*. NOAA Technical Report NMFS 66, National Oceanographic and Atmospheric Administration, Washington, D.C., 151 pp.
- Anderson, O.F., Bagley, N.W., Hurst, R.J., Francis, M.P., Clark, M.R. & McMillan, P.J. (1998) *Atlas of New Zealand fish and squid distributions from research bottom trawls*. NIWA Technical Report 42, National Institute of Water and Atmospheric Research, Wellington, New Zealand, 303 pp.
- Chirichigno, N.F. (1968) Nuevos registros para la ictiofauna marina del Peru. *Boletín Instituto del Mar del Perú*, 1, 380–503.
- Compagno, L.J.V. (2005) Checklist of living Chondrichthyes. In: Hamlett, W.C. (Ed.), *Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids and Chimaeras*. Science Publishers, Inc., Enfield, NH, pp. 503–548.
- Compagno, L.J.V., Stehmann, M. & Ebert, D.A. (1990) *Rhinochimaera africana*, a new longnose chimaera from southern Africa, with comments on the systematics and distribution of the genus *Rhinochimaera* Garman, 1901 (Chondrichthyes, Chimaeriformes, Rhinochimaeridae). *South African Journal of Marine Science*, 9, 201–222.
- Cox, A. (1983) Ages of the Galápagos Islands. In: Bowman, R., Berson, M., & Leviton, A. (Eds.), *Patterns of Evolution in Galápagos Organisms*. American Association for the Advancement of Science, San Francisco, CA, pp. 11–23.
- de Buen, F. (1959) Notas preliminares sobre la fauna marina preabismal de Chile, con descripción de una familia de rayas, dos géneros y siete especies nuevos. *Boletín del Museo Nacional de Historia Natural, Santiago, Chile*, 27, 171–201.
- Didier, D.A. (1995) Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). *American Museum Novitates*, 3119, 86 pp.
- Didier, D.A. (1998) The leopard *Chimaera*, a new species of chimaeroid fish from New Zealand (Holocephali, Chimaeriformes, Chimaeridae). *Ichthyological Research*, 45, 281–289.
- Didier, D.A. (2002) Two new species of chimaeroid fishes from the southwestern Pacific Ocean (Holocephali, Chimaeridae). *Ichthyological Research*, 49, 299–306.
- Didier, D.A. (2004) Phylogeny and classification of extant Holocephali. In: Carrier, J.C., Musick, J.A. & Heithaus, M.R. (Eds.), *Biology of Sharks and their Relatives*. CRC Press, Boca Raton, FL, pp. 115–135.
- Didier, D.A. & Nakaya, K. (1999) Redescription of *Rhinochimaera pacifica* (Mitsukuri) and first

- record of *R. africana* Compagno, Stehmann and Ebert from Japan (Chimaeriformes: Rhinochimaeridae). *Ichthyological Research*, 46, 139–152.
- Didier, D.A. & Rosenberger, L.J. (2002) The spotted ratfish, *Hydrolagus colliei*: notes on its biology with a redescription of the species (Holocephali: Chimaeridae). *California Fish and Game*, 88(3), 112–125.
- Didier, D.A. & Séret, B. (2002) Chimaeroid fishes of New Caledonia with description of a new species of *Hydrolagus* (Chondrichthyes, Holocephali). *Cybium*, 26, 225–233.
- Didier, D.A., Stahl, B.J. & Zangerl, R. (1994) Development and growth of compound tooth plates in *Callorhinchus milii* (Chondrichthyes, Holocephali). *Journal of Morphology*, 222, 73–89.
- Didier, D.A. & Stehmann, M. (1996) *Neoharriotta pumila*, a new species of longnose chimaera from the northwestern Indian Ocean (Pisces, Holocephali, Rhinochimaeridae). *Copeia*, 1996(4), 955–965.
- Ekman, S. (1953) *Zoogeography of the Sea*. Sidgwick & Jackson, London, 477 pp.
- Eschmeyer, W.N., Herald, E.S. & Hammann, H. (1983) *A Field Guide to Pacific Coast Fishes of North America*. Houghton Mifflin Company, Boston, 336 pp.
- Grogan, E.D. & Lund, R. (2004) Biology of sharks and their relatives. In: Carrier, J.C., Musick, J.A. & Heithaus, M.R. (Eds.), *Biology of Sharks and their Relatives*. CRC Press, Boca Raton, FL, pp. 3–32.
- Grove, J.S. & Lavenberg, R.J. (1997) *The Fishes of the Galápagos Islands*. Stanford University Press, Stanford, California, 863 pp.
- Leviton, A.E., Gibbs Jr., R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985(3), 802–832.
- Maisey, J.G. (1984) Chondrichthyan phylogeny: a look at the evidence. *Journal of Vertebrate Paleontology*, 4(3), 359–371.
- Maisey, J.G. (1986) Heads and tails: a chordate phylogeny. *Cladistics*, 2, 201–256.
- McCosker, J.E. (1997) A half mile down: figments of fancy off the Galápagos Islands. *Pacific Discovery*, 50, 42–45.
- McCosker, J.E. (1998) (Review of) *The fishes of the Galápagos Islands* by Grove, J.S. and Lavenberg, R.J., 1997. *Copeia*, 1998(3), 809–812.
- McCosker, J.E., Merlen, G., Long, D.J., Gilmore, R.G. & Villon, C. (1997) Deepslope fishes collected during the 1995 eruption of Isla Fernandina, Galápagos. *Noticias de Galápagos*, 58, 22–26.
- Miller, D.J. & Lea, R.N. (1972) Guide to the coastal marine fishes of California. *Fish Bulletin*, 157, 249 pp.
- Moura, T., Figueiredo, I., Bordalo-Machado, P., Almeida, C. & Gordo, L.S. (2005) A new deep-water chimaerid species, *Hydrolagus lusitanicus* n. sp., from off mainland Portugal with a proposal of a new identification key for the genus *Hydrolagus* (Holocephali: Chimaeridae) in the north-east Atlantic. *Journal of Fish Biology*, 67, 742–751.
- Patterson, C. (1992) Interpretation of the toothplates of chimaeroid fishes. *Zoological Journal of the Linnean Society*, 106, 33–61.
- Schaeffer, B. (1981) The xenacanth shark neurocranium with comments on the elasmobranch phylogeny. *Bulletin of the American Museum of Natural History*, 169, 3–66.